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THE CRANIAL MUSCULATURE AND THE ORIGIN
OF THE FRILL IN THE CERATOPSIAN
DINOSAURS.

By RICHARD S. LULL.

(With Plates I to III.)



ART. XLII.—*The Cranial Musculature and the Origin of the Frill in the Ceratopsian Dinosaurs*; by RICHARD S. LULL. (With Plates I to III)

DOLLO (1884) in his fifth note on the Dinosaurians of Bernissart has discussed the muscles of mastication of certain dinosaurs in comparison with those of a rodent, a crocodile, and a chameleon. This work has suggested to the writer a further study of the musculature of the skull, especially in the Ceratopsia, with a view of gaining an insight, if possible, into the origin of the peculiar defensive cranial armor of this remarkable group.

These studies are based more particularly on the type skulls of *Triceratops serratus* and *T. prorsus* Marsh which are preserved in the Peabody Museum at Yale, supplemented by an admirable palate, referred to the former species, in the American Museum of Natural History. The chief basis for comparative study has been the modern chameleon, which, as the author will show, exhibits some very remarkable points of convergence in structure toward the Ceratopsia.

PART I. *Musculature.*

Muscles of mastication.

The Iguanodont dinosaurs differed from all other reptiles in their method of feeding in that they were herbivores which *masticated* their food, thus requiring a development of muscles, especially the temporal, rare among reptiles. Chameleons, though insectivorous, and having the tongue for prehension, use the teeth, not for holding, but for chewing the firm-bodied Orthoptera and Lepidoptera which constitute their food. There is thus an analogy between the chameleons and the Iguanodontia in contrast to the carnivorous dinosaurs which, like the crocodiles, used the jaws for holding and tearing the prey rather than for mastication. The chameleons have enormous temporals, while in the crocodiles, as Dollo (1884) has shown, the temporals are relatively small and the pterygoid muscles, which in chameleons are feeble, are correspondingly large. In other words, the temporals are the larger in masticating forms; the pterygoids where the jaw function is largely one of resistance and, correlated with the development of the temporals, there is a corresponding development of the coronoid process of the jaw. In *Triceratops*, and other Ceratopsia, the jaw is powerful, articulated to a rigid suspensorium consisting of the quadrate, quadrato-jugal and the strong overlying jugal. The two dentaries meet in symphysis and their union is further strengthened by the massive prementary bone

which bore the lower beak. The teeth form an admirable chopping mechanism, shearing vertically past those of the upper jaw. The worn face of the entire tooth series, however, is not a perfect plane but is slightly twisted, being somewhat oblique at the posterior and becoming vertical at the anterior end of the row. The worn faces of the individual teeth exhibit in some instances tiny oblique striæ passing upward and backward across the enamel in those of the lower jaw. These would seem to indicate the direction of wear. The articulation of the jaw is such as to permit some freedom of

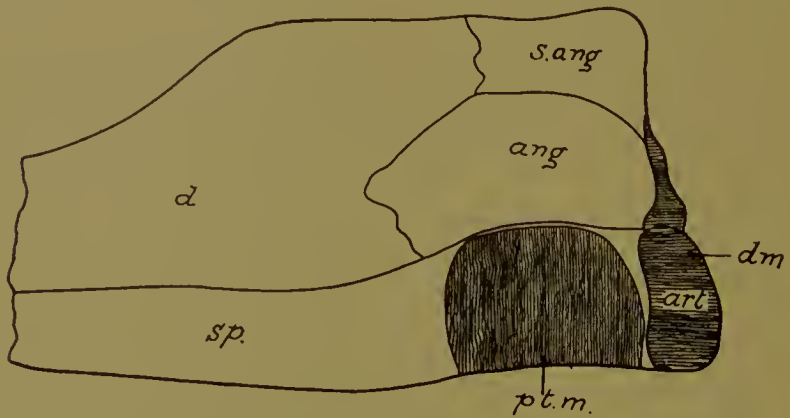


FIG. 1. Under side, rear, of lower jaw of *Triceratops*.

motion, and, judging from these facts, it would seem as though the jaw movement was in the main vertical, with a slight lateral motion either to the right or left at the beginning of the upward movement. When the final closure is reached the jaws would, however, be in perfect alignment, enabling the upper and lower beaks to form a perfect, turtle-like shear. There may have been a slight movement to the rear, which would account for the oblique striæ on the teeth; a forward movement would of course be out of the question on closure, as it would cause the wedge-shaped mechanism to bind.

Muscle insertions are indicated on the jaw, first on the rear margin of the very high coronoid process for the temporal muscle; on the inner lower margin of the splenial and dentary for the pterygoid muscles and on the lower face of the articular, angular, and splenial for the digastric or *depressor mandibuli* (fig. 1). A passage on either side leads upward and backward within the bones of the cheek, above the quadrate and exoccipital, and finally opens upon the upper surface of the frill through the *supratemporal fossa*. These are evidently the tracts wherein lay the temporal muscles, having

their origin on the dorsal surface of the parietals, one on each side of the median ridge of the frill and passing directly downward and forward to be inserted into the posterior margin of the coronoid process (Plate I). The direction of pull is met by that of the quadrate, whose oblique position is such as to withstand the strain to the best advantage. The high coronoid gives a long power arm which, though at an angle of 90° with the axis of the jaw, affords admirable leverage for the masticatory movements. The pterygoid muscles, both external and internal, must have been present; their direction of pull was more nearly vertical, and, while not strongly developed, they undoubtedly seconded the temporal muscle to a certain extent and guarded against dislocation.

A masseter muscle may also have been present having its insertion along the coronoid process just outside of that of the temporal and arising from the forward margin of the jugal bone.

The jaw was opened by means of the *depressor mandibulæ*, having its origin on the posterior and inner face of the quadrate, possibly to a certain extent on its outer face, as well as upon that of the quadratojugal. This was a rather broad, sheet-like muscle of moderate thickness and was inserted, as indicated above, into the lower aspect of the articular, angular, and splenial, possibly to a slight extent on the surangular. Cheek muscles must have existed, originating on the outer side of the maxillary and the posterior portion of the premaxillary as indicated by a sudden inward compression of the lower portion of these bones along a line running obliquely downward and forward from the jugal to the lower margin of the premaxillary bone. The insertion of this muscle lies along the forward margin of the coronoid and sweeps forward along the outer surface of the jaw, finally rising again to the end at the upper termination of the dentary-predentary suture. This broad sheet of muscle, probably equivalent to the buccinator, was subsidiary to mastication, as its chief function was to retain the food in the mouth. The extent of this muscle limits the backward extent of the gape of the mouth, as the writer (Lull, 1905) has shown in previous papers.

Muscles of the Neck.

The occipital condyle is hemispherical and fits into a correspondingly deep depression in the atlas. The extent of the two articular surfaces is so nearly equal that a very slight movement of the cervicals causes one facet to go past the limits of the other, as verified by actual experiment. This would seem to imply a very limited range of movement at this point, the hemispherical condyle being an ancestral feature retained

in order to allow a rotary motion of the skull, as the usual mechanism for permitting this movement, the articulation between the atlas and axis, by means of an odontoid process, is wanting, the first four cervicals being immovably coössified. The chief movement of the head seems to have been accomplished by the bending of the neck as a whole. The normal posture of the head was depressed, the muzzle coming rather near the ground. The proof of this lies in the fact that the condyle is borne on a stalk or peduncle which is bent downward at an angle with the longitudinal axis of the skull. If the cervical vertebræ are not in line with the axis of the condyle, it not only produces what engineers call an "invert joint", an extremely weak structure mechanically, but the articular facets no longer coincide. Plate II serves to illustrate this matter.

The ring-like atlas bears no transverse or other processes, which, together with the fact that movement of the anterior cervicals is so limited, makes it probable that some of the muscles which are ordinarily inserted into the atlas have been transferred to the occipital region of the skull. The rear of the skull and the inferior surface of the frill exhibit a number of well-developed muscle depressions which may be interpreted as follows:

The basioccipital shows, on either side of the median line beneath, a deep depression, the insertion of the *rectus capitis anticus longus* (*rl*) muscle, which has its origin on the ventral aspect of the cervical vertebræ from the axis backward (Plate II). This doubtless served to depress the skull and was a muscle of moderate power. Smaller depressions, also in the basioccipital, lying without the first mentioned, seem to have been the insertions of the *rectus capitis anticus brevis* (*rb*), the origin of which was on either side of the axis. This was also a depressor muscle of the skull as well as one which swayed it from side to side but was relatively feeble, being in all probability passively resistant rather than active in its function. On either side of the foramen magnum may be found small depressions evidently for the insertion of the *rectus capitis posticus minor* (*rm_i*), which in the turtle arise from the neural arch and diapophyses of the atlas. In *Triceratops* the point of origin was probably shifted backward to the axis.

Above, the supraoccipitals show large depressions into which were inserted the *rectus capitis posticus major* (*rma*) muscles, which arose from the neural spine of the axis. These were muscles of considerable volume and aided in raising, or rather in supporting the head. Thus there seem to have been, as in the turtle, four pairs of muscles running from the anterior cervicals

to the occipital bones, of which the dorsal and ventral ones were powerful, the lateral ones relatively feeble.

Just above the foramen magnum in the supraoccipital bone lie two deep depressions separated by a thin lamina of bone. These are continuous with a median groove on the ventral surface of the parietal extending backward about two-thirds of the distance toward the margin of the frill. Along the center of this groove lies a slight ridge running backward for about half its distance, the precise extent being variable. This ridge is continuous with the lamina which divides the depressions in the supraoccipital. In the two specimens of *Triceratops serratus* the parietal groove fades out toward the rear, while in *T. prorsus* it ends abruptly and is quite deep at the posterior end. Just beneath this groove when the cervicals are *in situ* lie the neural spines of the second, third, and fourth vertebrae, which are depressed backward so as to lie nearly parallel with the under surface of the frill. There can be no question that we have here the insertion on the skull of the *complexus major* muscles, which arose from the cervical spines and expanded upward and forward in a pair of relatively thin sheets as in the chameleon. These muscles were of prime importance, not alone in fulfilling the function of the *ligamentum nuchæ* of the mammal, but also from a developmental standpoint, as will ultimately be shown. They served to maintain the poise of the skull and were probably, as in recent reptiles, continuations of the *longissimi dorsi* which run the length of the back. At the extremities of the exoccipitals and upon the adjacent ventral surfaces of the squamosal bones are large, depressed muscle areas which were confluent. These, if taken collectively, were the insertions of the largest muscle masses of the neck, those which, lying as they did in the wake of the supra-orbital horns, bore the brunt of the strain, in wielding these powerful weapons (*vide infra*, p. 395). It is somewhat difficult to homologize these muscles with accuracy but they must have included the *complexus minor*, the anterior prolongation of the *latissimus dorsi*, the insertion of which is normally in the exoccipital. The under surface of the frill shows other somewhat variable depressions, notably in the parietal bone near the squamosal suture. These are well out toward the periphery of the frill (Plate III). I am not sure of their identity, but it is reasonable to suppose that the whole neck of the creature must have been enormously muscular, covering the entire lower surface of the frill except for its free margin, the extent of which is a specific variation).

From the frequency with which one observes injuries, perforations and fractures, upon the ceratopsian skull, I cannot believe that the powerful armament of the horns was for mere

passive defense. Many of the injuries are such that none other than a Ceratopsian could have inflicted them, and this, together with the fine mechanical development of the great muscles, especially those in the wake of the supraorbital horns, shows that, in spite of apparent unwieldiness, *Triceratops* was an aggressive fighter when thoroughly aroused. In the type skull of *Diceratops hatcheri* Lull (1905) in the United States National Museum, the so-called foramina through the anterior part of the squamosal bones almost entirely obliterate the insertion of the *complexus minor* muscle of the left side, and partially obliterate that on the right. Enough, however, remains to indicate that the muscle depressions were precisely as in *Triceratops*. This strengthens the conviction which the writer has always had, that these perforations are entirely pathologic; moreover, the wounds must in large measure have disabled the animal and may ultimately have caused its death, though it lingered on long enough for the broken margins of the bone to heal, a matter of a few weeks.

PART II. *Origin of the Crest.*

The crest, which is so characteristic of the Ceratopsia, has its parallel in the so-called casque of the chameleon skull. The

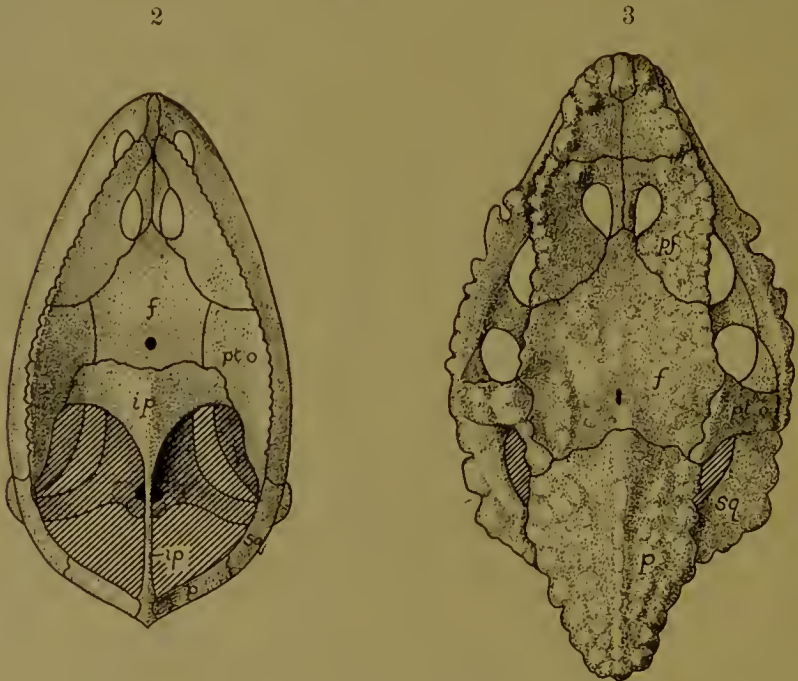


FIG. 2. *Chameleo vulgaris*; adapted from Parker.
 FIG. 3. *Chameleo pumilis*; " " "

latter, however, while variably developed in different species of chameleons, never reaches the extreme degree of perfection which was attained by *Triceratops*.

In the chameleon the casque generally contains five bony elements: a median interparietal, two lateral squamosals, and, connecting these in the rear, a pair of slender parietal bars (fig. 2). These structures enclose two lateral supratemporal fossæ generally of large extent, though in some species, as *Chameleo pumilis* (fig. 3), much reduced owing to the great development of the parietal elements of the crest. (Parker 1881, p. 97.) In the *Triceratops* the crest contains the same elements except that the parietal region is composed of but one bone, no trace of sutures having been found as yet. Here the supratemporal fossæ are relatively small and do not lead directly through the crest or frill but downward and forward

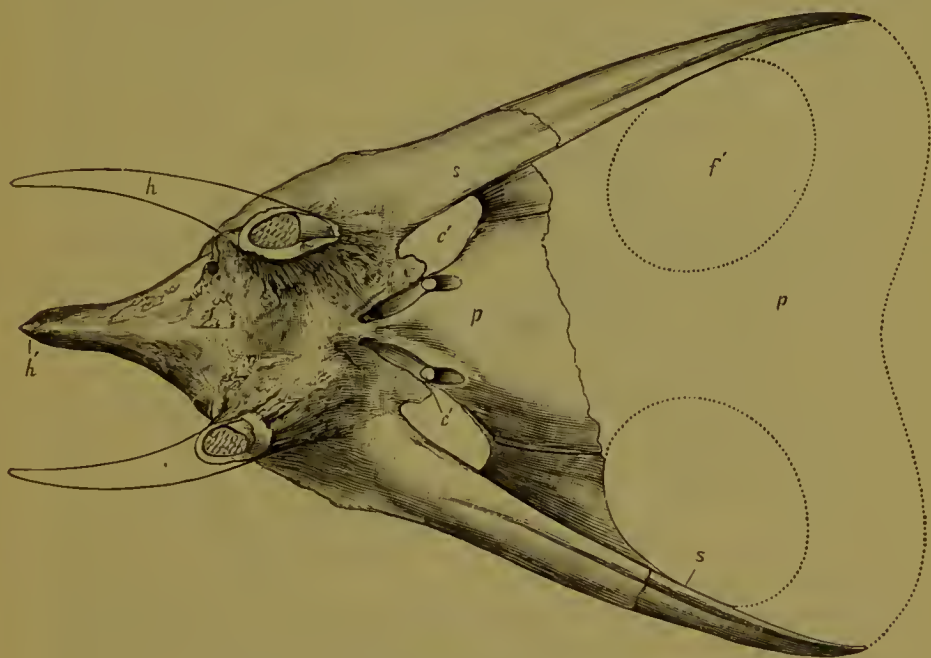


FIG. 4. *Torosaurus latus*; skull, top view.

beneath the postfrontal bones and above the exoccipitals and jugals into the spacious cavities within the false roof of the skull (*vide infra*, p. 395), fig. 6.

In the Judith River genera, *Ceratops*, *Monoclonius*, and *Centrosaurus*, and in *Torosaurus* of the Ceratops beds, the crest is perforated by a pair of relatively immense parietal fenestræ, absent in *Triceratops* and its near relative *Dicera-*
tops. These fenestræ seem at first sight to be the equivalents of the supratemporal fossæ of the chameleon, as their relationship with the bony elements of the frill is practically the same. This I believe to be partially true: the fenestræ in the Cera-

topsia representing the space between the median and lateral elements of the parietal region which has been constricted off from the present supratemporal fossæ by a union of the parietal elements at their anterior end. Evidence in favor of this view is seen in the type specimen of *Torosaurus latus* Marsh, here figured (fig. 4), in which a distinct suture may be seen on either side leading from the parietal fenestra forward to the supratemporal fossa and representing the line of final closure of the bony bridge separating the two openings. *Torosaurus gladius* Marsh has a faint indication of the same suture, thus exhibiting a greater degree of specialization than its ally. *Centrosaurus apertus* Lambe from the Judith river beds also has indications of the same suture (fig. 5), while in the specimen of *Monoclonius crassus* Cope from the same horizon the suture probably existed if indeed the closure was complete.

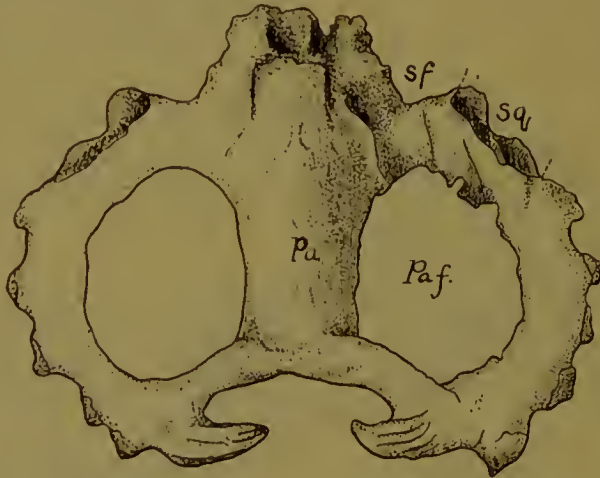


FIG. 5. *Centrosaurus apertus* Lambe; modified from Lambe.

The bone is fractured at this region, unfortunately in the only known specimen, so that this question cannot be decided. In *Ceratops canadensis* Lambe, also from the Judith river, the squamosal is relatively much larger than in most of its contemporaries and the lateral element of the parietal, the only part preserved, is a slender bar of bone which did not unite with the median element forward (fig. 7). It is probable, however, that the shutting off of the fenestra from the supratemporal fossa was effected by the widening of the anterior portion of the median parietal element to meet the squamosal. In *Triceratops* the final closure of the parietal fenestrae is effected by a continuous growth of bone over the entire parietal region of the frill (fig. 6). This bone is, however, extremely thin in what would be the anterior

part of the fenestra if it were present and which probably represents the point of final closure of that aperture.*

There is a very precise analogy between the crest of a chameleon and that of the Ceratopsia, as it is primarily, in each instance, merely a backward extension of the parietal segment of the skull to obtain a greater area for the origin of the temporal muscles. This backward extension of the median region especially gave greater area for the *complexus major* muscles, which could then extend from their old insertion on the supra-occipital backward along the interior surface of the median parietal bar (interparietal), giving greatly increased leverage in wielding the head.

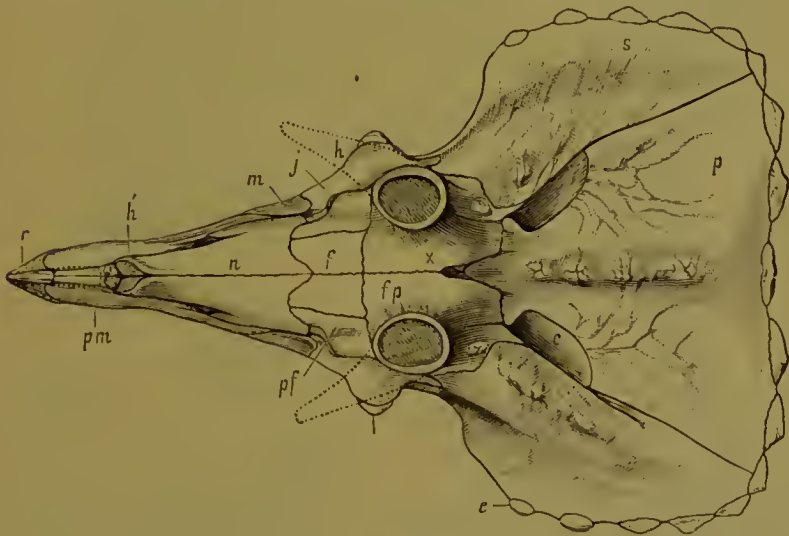


FIG. 6. *Triceratops serratus*.

There seems to be an interesting correlation between the development of the squamosal elements of the frill and that of the paired horns. The broadening squamosals evidently increased in size to allow for the extension of the great lateral muscles of the neck from their original insertion on the exoccipitals (*vide supra*, p. 391). This not only provides for larger and more powerful muscles, but also gives greater leverage in wielding the supraorbital horns. *Centrosaurus apertus* Lambe (1904) (fig. 5) had a straight, powerful nasal horn, evidently its chief weapon, and extremely small squamosals, as shown by the very short parieto-squamosal suture, the major part of the crest being composed of the parietal elements. In the Judith

* *Triceratops* and *Torosaurus* it must be remembered, while contemporaneous, are not directly related, but represent parallel races derived independently from Judith river ancestry. In *Torosaurus* the parietal fenestræ were persistent. (Lull, 1908, p. 101.)

River *Ceratops canadensis* Lambe (1904) in which the supra-orbital horns are powerful, backwardly curved weapons, the squamosals are large, as shown in figure 7. The squamosals are important elements of the frill in all of the later genera, in which the nasal horn is retrogressive and the supraorbitals all important.

Though primarily to provide muscular insertion and leverage, the protective function of the frill was gradually assumed. First along the spine, then along the area of the great veins and arteries of the neck and finally as a complete armor for



FIG. 7. *Ceratops (Monoelonus) canadensis* Lambe ; after Lambe.

the entire neck. In *Torosaurus* this final condition was never reached even though the offensive armament was fully equal to that of *Triceratops*, while in the last mentioned type the ideal frill was attained with its flaring margin armed with epoccipital bones, giving it a serrated edge which may have aided in aggressive warfare. (Compare figs. 4 and 6.)

All Iguanodont skulls which the author has seen exhibit a rudimentary crest, with its primary function of attachment for the temporal muscles; but only in the Ceratopsia has the backward extension for wielding the head and finally for protection of the neck been attained among dinosaurs. (Figs. 8, 9.)

PART III. *Convergencies.*

The distinctively Ceratopsian features are mimicked in a most remarkable manner by other reptiles, notably the turtles and chameleons.

With the turtles the features in common are the upper and lower beak and the curious false roofing of the skull above the brain case, so that both the turtles and Ceratopsia give the

impression of a mental capacity far beyond the actual size of the brain. In each case the large, seemingly massive skull is composed of extensive plates of bone bridging over cavernous spaces within, giving great superficial extent for mechanical needs with comparatively little expenditure of osseous material.

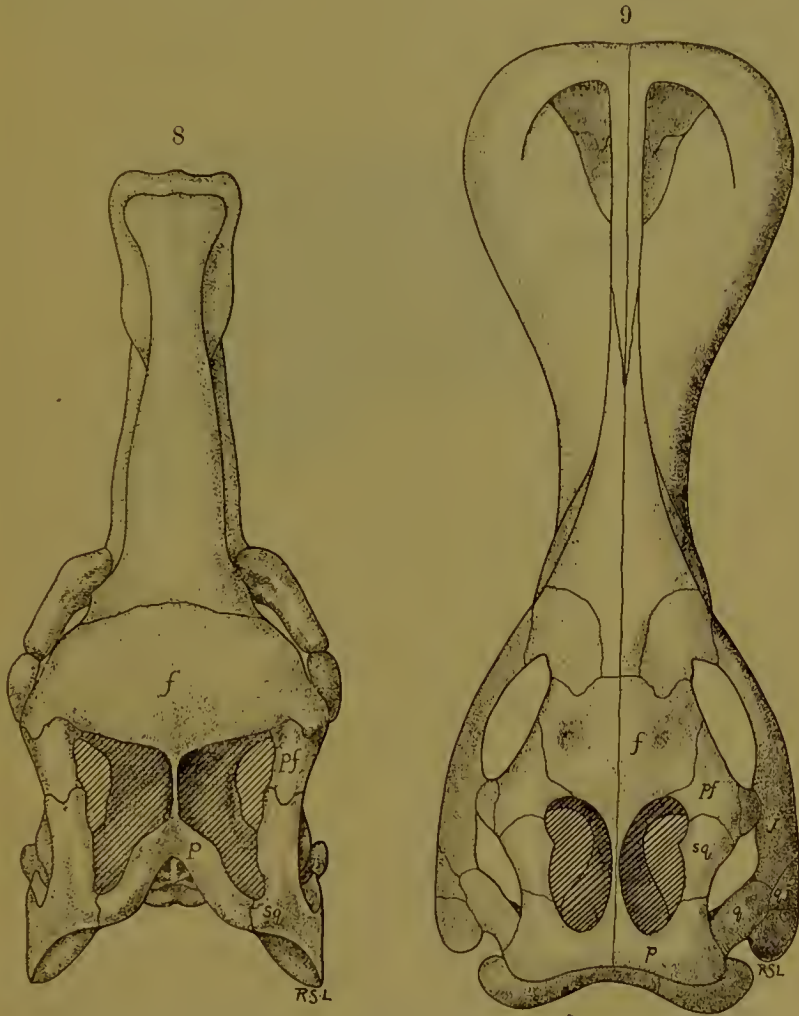


FIG. 8. *Iguanodon bernissartensis*; adapted from Dollo.
 FIG. 9. *Trachodon mirabilis*; after Cope.

Meiolania, a chelonian from the Pleistocene of Lord Howes Island and Queensland, has even developed horns, at first sight extremely suggestive of those of the Ceratopsia though situated too far back over the occiput for a precise homology.

The most interesting instances of convergence are with the chameleons, the likeness of whose casque to the Ceratopsian crest has been emphasized. The Dwarf chameleon *C. pumilis*

(fig. 3) has perhaps the most *Triceratops*-like crest, but the culmination is seen in the male of the little *Chameleo owenii* from Cameroon (fig. 10), as it not only has a fairly perfect frill but three horns as well, one upon the nose and a pair above the eyes precisely as in *Triceratops*. There is, however, this distinction; the horns in the chameleon are entirely epidermal, having no bony horn cores, and are confined to the male, whereas a hornless *Triceratops* has never been found. In



FIG. 10. *Chameleo owenii*; adapted from Metcalf.

Chameleon they seem to be the result of sexual selection and are certainly not for aggressive warfare in a creature which moves with the utmost caution, while in *Triceratops* the presence of efficient weapons in both sexes was an imperative factor in the struggle for existence.

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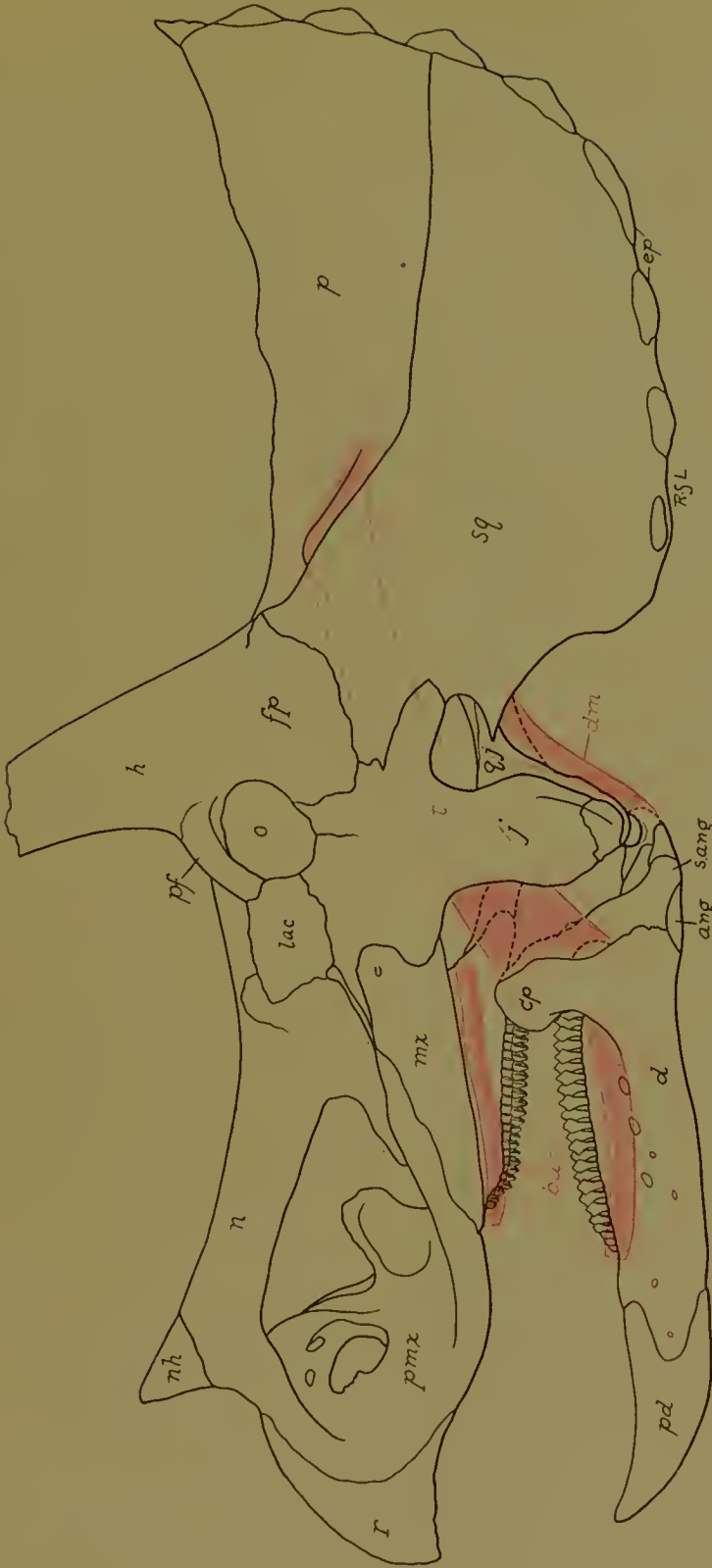
EXPLANATION OF PLATES AND FIGURES.

- PLATE I. Skull of *Triceratops serratus* Marsh, with jaw muscles (1/8).
 PLATE II. Skull of *Triceratops serratus* Marsh, with neck muscles (1/8).
 PLATE III. Skull of *Triceratops serratus* Marsh, rear view, with muscles (1/8). (Blood vessel impressions indicate the free margin of the frill.)

Bones: *ang*, angular; *bo*, basioccipital; *cp*, coronoid process; *d*, dentary; *ep*, epoccipital; *exo*, exoccipital; *fm*, foramen magnum; *fp*, postfrontal; *h*, supraorbital horn; *j*, jugal; *lac*, lacrimal; *m*, maxillary; *n*, nasal horn; *o*, orbit; *oc*, occipital condyle; *p*, *pa*, parietal; *pd*, prementary; *pf*, prefrontal; *pmx*, premaxillary; *qj*, quadratojugal; *qu*, quadrate; *r*, rostral; *sang*, surangular; *sq*, squamosal; I, atlas; II, axis; III and IV, 3d and 4th cervical vertebræ.

Muscles: *buc*, buccinator; *dm*, depressor mandibuli; *ip*, pterygoideus; *lat*, complexus minor (latissimus dorsi); *lc*, levator claviculæ; *lon*, complexus major (longissimus dorsi); *rb*, rectus anticus brevis; *rl*, r.a.longus; *rma*, rectus posticus major; *rmi*, r.p. minor; *t*, temporalis.

- FIG. 1. Under side, rear, of lower jaw of *Triceratops serratus*.
 FIG. 2. *Chameleo vulgaris*, adapted from Parker.
 FIG. 3. *Chameleo pumilis*, adapted from Parker.
 FIG. 4. *Torosaurus latus*, skull, top view, after Marsh.
 FIG. 5. *Centrosaurus apertus*, frill top view, modified from Lambe.
 FIG. 6. *Triceratops serratus*, skull, top view, after Marsh.
 FIG. 7. *Ceratops canadensis*, portion of skull, side view, after Lambe.
 FIG. 8. *Iguanodon bernissartensis*, skull, top view, adapted from Dollo.
 FIG. 9. *Trachodon mirabilis*, skull, top view, after Cope.
 FIG. 10. *Chameleo owenii*, adapted from Metcalf.
c, *sf*, supratemporal fossa; *f*, *paf*, parietal fenestra; shaded area, supratemporal fossa.

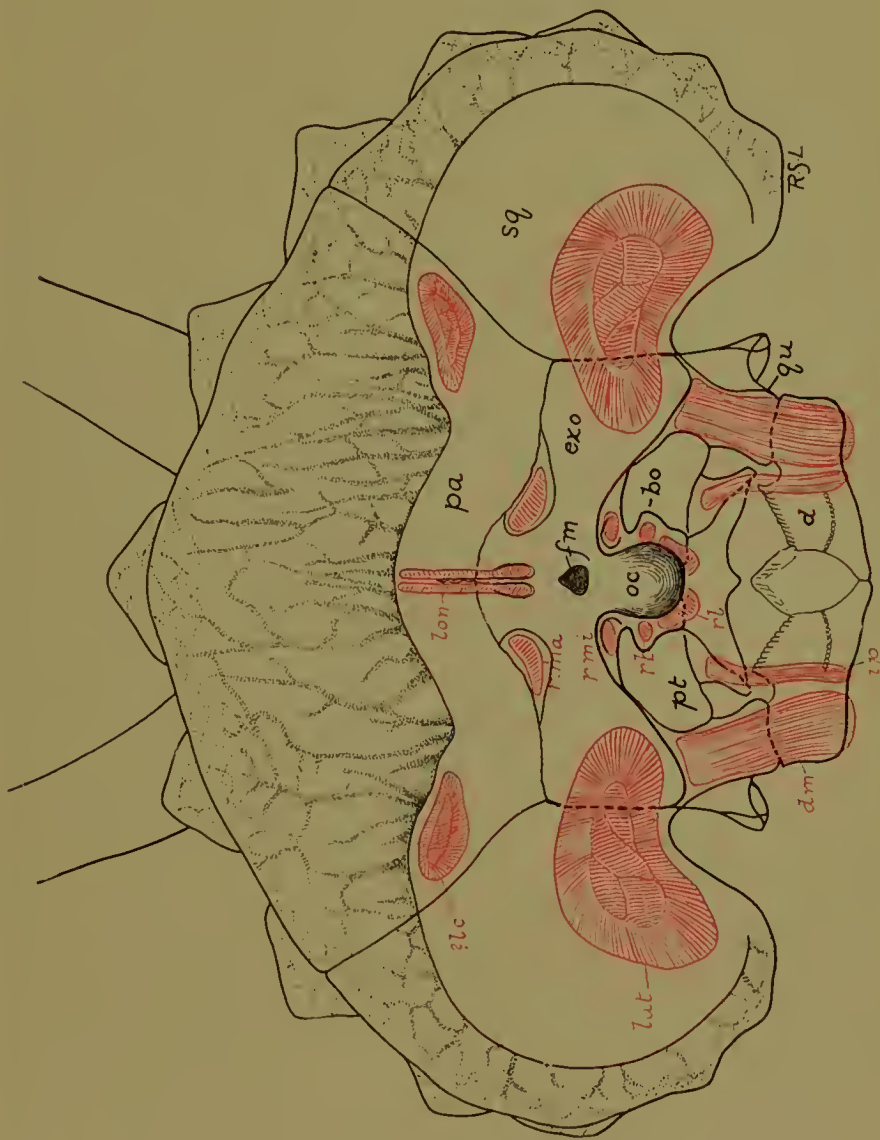


Skull of *Triceratops serratus* Marsh, with jaw muscles.



Skull of *Triceratops serratus* Maush, with neck muscles.





Skull of *Triceratops serratus* Marsh, rear view and muscles.

